this metamorphosis in almost all the embryos. Does this transformation of the ciliated embryo into a young *Acineta* always take place? It is allowable to doubt this; twice I have seen ciliated embryos become enclosed in a cyst, instead of changing into young *Acinetæ*. I was unable to carry the observation further, and ascertain whether or not the Infusorium underwent new transformations in the interior of the cyst. Further researches are required to clear up this obscure question.

II.—*On the Development of the Vegetable Ovule called 'Anatropous.'* By John Miers, F.R.S., F.L.S., &c.

Although the changes that take place in the development of the vegetable ovule have long since occupied the attention of the ablest physiological botanists, it is evident that the real nature of its mode of growth is not yet well understood. My first object therefore is to show that the doctrine upon this important subject, as taught in the best elementary works, is founded upon a very grave error. I was led into this inquiry by my desire to ascertain the nature of the fleshy covering enveloping the hard tunic in certain seeds *, and which appeared to me arilloid in its nature. This was contested by Dr. Asa Gray, who considered these two very opposite kinds of tunics as one baccate testa, both deriving a common origin from the primine of the ovule†. To this view I was unwilling to subscribe; and in my subsequent discussion of the subject, trusting fully to the orthodoxy of the common creed of botanists on the development of the ovule, I argued ‡ that the fleshy covering in question must be an expansion or growth of the placentary sheath, because it enclosed the raphe: and so it is undoubtedly—but not in the light of an extraneous expansion, as I then viewed the question. This induced me to examine, by personal observation, the actual progress of growth of the ovule in certain plants which produce what have been called anatropal seeds; and I soon became convinced that I had been led into an error of inference, solely by my faith in the universally prevalent creed. Having lately completed the investigation of many *Rhamnaceous* and *Anacardiaceous* seeds, in which several novel points of structure have been observed, which are difficult to explain, I am desirous, before the publication of these results, that the real nature of the development of the ovule should be well understood. I therefore now proceed to show that the doctrine upon this subject, as at present taught, is completely fallacious.

* Trans. Linn. Soc. xxii. 81.
† Journ. Linn. Soc. ii. 106.
‡ Ann. Nat. Hist. 3rd ser. i. 276.

It is important to observe, that the late Mr. R. Brown, to whom science is so greatly indebted for his grand discoveries on this subject, and who in simple language first explained the nature of the changes that take place in the development of the ovule*, does not describe the mode of action objectionably assumed in the writings of physiological botanists; and it is worthy of remark that he never adopted the nomenclature founded upon the doctrine here alluded to†.

To Brongniart, who pursued these great discoveries, the highest merit is due for his able and patient investigation‡ into the nature of the pollen, the peculiar structure of the stigmatic tissues, the mode in which the pollinic influence is conveyed into the ovary, the structure of the ovule, of its proper tunics, and of the nucleus, the development of the embryo-sac, the production of the embryo, and the means by which the seed is finally perfected. It is also deserving of notice, that in all these careful investigations, no allusion is anywhere made to the inversion of the nucleus, or to any excentric growth of the original tunics that might effect the kind of inversion since assumed to take place in an anatropal ovule. It is true that both he and Mr. Brown commenced their researches upon the ovule from the moment it is ready to receive the pollinic influence; but had either of these careful observers witnessed any such previous action of growth, they would not have failed to allude to the subject.

Mirbel, who confirmed and extended these interesting researches in his celebrated memoir on the development of the ovule §, has received the highest eulogiums from all quarters, for the benefit which these discoveries rendered to science; but it appears to me that the greatest share of this merit is due to Brown and Brongniart, who preceded him in these inquiries. Much praise is certainly due to Mirbel for the lucid manner in which he repeated and confirmed the facts already brought to light by those who preceded him, and also for tracing the growth of the nucleus and ovular coats from their first appearance,

* Appendix to King's Voyage, p. 43.

† The way in which Mr. Brown uses the term *inverted* is in a comparative sense: *loc. cit.* p. 52, where he says, "the inner membrane is inverted with respect to the external umbilicus," or, in other words, that the chalaza is opposed to the hilum; but he does not allude to any *action of inversion* of the ovular tunics.

‡ "Mémoire sur la Génération et le Développement de l'Embryon dans les Végétaux Phanérogames." Ann. Sc. Nat. xii. pp. 14, 145, 225, tab. 34—44: read before the Academy, Dec. 28, 1826.

§ "Nouvelles Recherches sur la Structure et les Développemens de l'Ovule végétale." Mém. de l'Acad. ix. p. 609: lu à l'Académie 28 Dec. 1828. Additions dans un 2nd mémoire lu 28 Dec. 1829; *idem*, p. 629. planches 1–10.

which his predecessors had not noticed; but his greatest claim to distinction rests upon the nomenclature which he devised in order to express the changes observed, which will make his name prominent in the annals of embryology. It is, however, deeply to be regretted that the more original matter contributed in that memoir, or rather, his explanations of the facts there related, should have laid the foundation of the great error in the history of these developments, the fallacy of which I now proceed to demonstrate.

In order that I may be free from the blame of misrepresenting this subject, I will here quote from the following authorities the doctrines they have severally published.

Mirbel says (*loc. cit.* p. 612) that the *anatropal* ovules "*se renversent tout entiers,* et durant *ce mouvement de conversion* le raphé se développe avec la primine, et *transporte le hile de la base de l'ovule à son extrémité supérieure*; ce sont les Anatropes; mais le développement du raphé fait que le *hile* s'éloigne de la chalaze, et *va prendre place* à côté de l'éxostome" (micropyle). He says again (p. 631), "Le funicule, dans un grand nombre des espèces, *se soude longitudinalement* à la primine depuis l'endroit où il forme la chalaze, jusqu'à une distance plus ou moins éloignée d'elle. *Alors* il se montre à la superficie de la primine comme une ligne en relief, qui se termine à la base de l'ovule; cette ligne est le raphé; mais quand il n'y a peu d'adhérence entre la primine et le funicule que là même où les vaisseaux funiculaires pénétrent dans la secondine, la chalaze se confonde avec le hile, qui est le point d'attache du funicule sur la primine, et la place manque pour un raphé." Again (p. 649), "Quand un ovule tend à l'anatropie, la chalaze, c'est-à-dire l'extrémité du funicule, se porte en avant, non dans la direction de l'axe, mais dans une direction un peu oblique, et en suivant une ligne courbe, qui par sa partie supérieure se rapproche insensiblement de l'axe, et tandis que ce mouvement s'opère, *le sommet par un mouvement inverse se dirige vers la place que la base a abandonnée. Il y a donc échange de position entre les deux extrémités de l'axe de l'ovule; cette axe, poussé obliquement par la chalaze, semble se mouvoir comme une aiguille de boussole que l'on ferait tourner sur son pivot.* Mais la chalaze n'étant que le bout du funicule, l'évolution ne saurait s'opérer sans un allongement de ce cordon, égal au moins à la longueur de l'axe de l'ovule."

If we examine the series of progressive analytical drawings by which these changes are demonstrated in that celebrated memoir, we find that the figures are diametrically in contradiction to the explanations. The former, which portray the facts as he saw them, offer the more reliable testimony of the real truth: for example, in plate 3, showing the progressive growth of the

anatropal ovule of *Aristolochia,* fig. 1 is a simple pullulation from the placenta, the rudiment of the primine, or what I have called the placentary sheath, because it encloses in its tissues the nourishing vessels that terminate in a certain budding point, and that form the future raphe; it is not the nucleus, as is generally taught. Close to the extremity of this, out of a circular depression, the first appearance of the nucleus is exhibited in fig. 2. The secundine next presents itself in the same hollow, surrounding the base of the nucleus in fig. 3. After this we observe the gradual swelling of the under part of the nuclear support, or the downward growth of the placentary sheath, which becomes the primine, in the form of a bag suspended by the remaining stipitate portion of the sheath or funicle,—the original margin of the depression first described remaining as the mouth of this bag, and constituting the foramen of the primine (micropyle or exostome), which from first to last never changes its position or its aspect—a most important point to be observed. During this action of centrifugal growth, the chalaza, or place of attachment of the nucleus, necessarily recedes from its original position, remaining at the bottom of the growing bag or primine, the extension of the nourishing vessels keeping pace with its *downward* growth, and still terminating in the now basal chalaza; at the same time, the enclosed nucleus and secundine severally grow *upwards,* both constantly attached to the budding or chalazal point of their origin: all this is seen in fig. 5, which represents a perfect ovule ready to receive the pollinic influence. We find in fig. 6 exactly the same disposition of the parts after the ovule has been impregnated, and when the embryo-sac with the nascent embryo has been developed. In these several stages we perceive that the foramen of the primine, the mouth of the secundine, and the apex of the nucleus, from first to last, all culminate towards one common point, while the basal portions of the same parts as constantly point downwards: if the expression may be allowed, they all retain the same uniform polarity; there is *no inversion* in any of the parts, or even an approach to it; *the hilar or funicular point* of attachment *is not transported from the base of the ovule to its superior extremity,* as asserted; and there is *no agglutination* (*soudure*) *of the primine to the cord of the raphe,* elongated by this assumed act of semirevolution of the ovule. In fine, although the mode of growth, as shown in the drawings, is perfectly correct, there is throughout the whole description a misconception, and a complete mistake in the use of all the terms employed by Mirbel, especially in those I have denoted by italics. The same mode of growth is again still more fully demonstrated in plate 7, in the instance of *Tulipa.* Nowhere among the other numerous exemplifications in

this celebrated memoir can we find any material variation in the direction of the parts of an anatropal ovule: this only exists in campylotropal or amphitropal ovules, where, of course, owing to the curvature of the several parts, from an excessive one-sided growth, a more or less partial inversion takes place.

The same erroneous description is given by the able St.-Hilaire in his 'Morphologie Végétale' (p. 540), where he thus defines the development of an anatropal ovule. Its first appearance upon the placenta is a small protuberance (wrongly said to be the *nucleus* of the future ovule), which by degrees becomes covered by two cups that rise successively from its base and form the future tunics, primine and secundine. The so-called "ovules anatropes, par la *courbure* graduelle de la *base de leur axe*, se rapprochent peu à peu du cordon ombilical, et après avoir *décrit un demi-cercle, le rencontrent, se soudent* avec lui, et le confondent en quelque sorte dans leur substance; souvent le cordon, *ainsi soudé*, se montre comme une proéminence extérieure, mais souvent aussi il ne se laisse point apercevoir; *la partie soudée* du cordon porte le nom raphé." In order to impress this action more forcibly upon the conviction of his readers, St.-Hilaire compares the ovule so developed, to a monopetalous flower in bud, which is made to perform half a revolution, by being inverted and suddenly bent down close to its base, with its peduncle agglutinated to the calyx and corolla; here the calyx and corolla assume the position of the tunics of the ovule—its ovary, the nucleus—and their common base of union, the chalaza,—the pedicel representing the raphe.

A very similar explanation of the anatropy of the ovule is given in the excellent work of Adr. de Jussieu (Cours Élémenmentaire, p. 343), where his definition is aided by figures. Fig. 1 is again erroneously said to be the *nucleus, first developed*; fig. 2 the same, with the primine next appearing; fig. 3 the same, more advanced, with the addition of the second coat (secundine). "Le développement ne marche pas ainsi égal de tous les côtés; *sur l'un il est très-prononcé*, tandis qu'il reste à peu près *stationnaire sur le côté opposé*. Par là, *la pointe* de l'ovule, avec son micropyle *tourné primitivement en haut, se tourne de côté*, puis un peu plus tard en dehors, *puis enfin tout à fait en bas* (fig. 4) *après avoir fait ainsi un demi-tour de révolution*. *La chalaze* emportée de même avec les tégumens qui s'étendent, et conservant ses rapports avec le micropyle, *fait une révolution analogue*, mais en sens inverse, *et marche de bas en haut*, de manière qu'elle s'éloigne de plus en plus du hile, dont le micropyle au contraire s'est rapproché de plus en plus." Fig. 5 shows a section of the same ovule, where it is explained how "le faisceau vasculaire qui aboutissait à la chalaze, la suit dans sa révolution en s'allongeant,

et ce prolongement forme le raphé." I was led into error of argument, as I have mentioned, solely by my faith in the truth of this last consideration, a doubt of the correctness of which never crossed my mind, taught as it was by such eminent authorities.

The definition of Prof. Lindley (Introd. p. 180) is less explicit, and therefore less objectionable; but he evidently entertained a similar view, though expressed in different terms. He states that in this kind of ovule "*one of its sides grows rapidly, while the opposite side does not grow at all,* so that the *point* (foramen) of the ovule *is gradually pushed round to the base,* while, correspondingly, *the base of the nucleus is removed from the hilum to the opposite extremity*; and when this process is completed, *the whole of the inside of the ovule is reversed.*" It is needless to repeat that this definition is founded upon misconception, or on too much faith in the erroneous descriptions of Mirbel and St.-Hilaire.

Dr. Fritsche (in 1835) was the first who impugned in part the accuracy of Mirbel's observations on the development of the ovule in *Cucurbita*. Mirbel had described the first indication of the growing ovule as a simple cylindrical shoot protruding from the placenta, which after a while exhibits a point, somewhat excentrically placed near its apex, out of which the nucleus forces an opening; this nucleus continues to grow, becoming surrounded at its base by an annular ring, the rudiment of the secundine, while the lacerated opening out of which the nucleus springs forms the mouth of the primine and gives rise to the outer coat of the ovule. Fritsche confirms the accuracy of the appearances thus described, but contends* that the nucleus does not originate in a sort of coleorhizal protrusion as narrated by Mirbel, but that the whole placental shoot in question is in reality the nucleus upon its funicular support, before any indication of the primine and secundine: this shoot is covered by a single epidermal layer of cellular structure; and at some little distance from its extremity a double circular constriction is formed, thus leaving a prominent annular ring round the papilla, which remains as the nucleus, while the portion of the epidermis between the two strictures separates from the internal parenchyma and becomes plicated, so that its folded surfaces unite together in the form of a short tube, thus giving origin to the future secundine. Subsequently that portion of the epidermis below the strictures also separates and becomes folded in like manner, thus giving rise to the future primine. This assumption of the separation of the epidermis I believe to be quite erroneous, for reasons presently to be given; and it will

* Wiegmann's Archiv, i. 2 Band, p. 229.

be seen that, in regard to this early stage of the development, Mirbel was nearer the truth than his opponent.

Schleiden, although he seems to have adopted the erroneous views of Fritsche concerning the earliest origin of the nucleus and ovular tunics, gave (in 1843) an account of their subsequent development and growth, somewhat different from that of Mirbel: he says*, "The funiculus is much elongated, the nuclear papilla bends downwards; and thus the side, either of the naked nucleus or of the simple or of the external bud-integument (secundine or primine), turned towards the funiculus, becomes blended with it. In the perfect seed-bud the nuclear papilla then lies close to the point of attachment, the chalaza opposite to it, and the line from the centre of the chalaza through the middle of the nucleus is straight: such a bud is termed reversed (*gemmula anatropa*); the adherent part of the funiculus is termed the raphe." Schleiden further aptly remarks—"Excepting Fritsche, not a single botanist has done anything on this weighty point of our subject, not even so much as to re-examine the researches of the distinguished Mirbel and Brown; and we find in consequence, even up to the most recent dates, the false views of Mirbel (and these often sadly disfigured) copied without reflection."

Prof. Henfrey (in 1847), in his truly excellent 'Outlines of Structural and Physiological Botany' (p. 199), thus defines the nature of the anatropal ovule:—"The nucleus is sometimes so affected by the development, that the apex or micropyle comes to be placed next the hilum, and the organic base of the ovule (the chalaza) at the opposite extremity; the vascular cord communicating with the chalaza is extended during the growth of the ovule, and the chalaza thus always communicates with the funiculus by these vessels, which run in the thickness of the coats, in the exterior where there are two. This cord is called the raphe, looking like a prolongation of the funicle adherent to the side of the ovule, and disappearing at the point, which is the organic base." This description, as far as it goes, is the clearest and most truthful detail of the development of the ovule yet given, as it does not allude to any presumed action of the inversion of the nucleus and its ovular coats, upon which all other accounts are more or less based. This scientific botanist, however, appears subsequently (in 1858) to have adopted the prevalent error in contending that "the inversion of the (anatropal) ovule takes place by a one-sided development of the tunics†."

Prof. Asa Gray has lately pursued this inquiry (in 1857) in

* Principles of Scientific Botany, Engl. edit. p. 390.

† Ann. Nat. Hist. 3 ser. i. 356.

a very philosophical spirit, in his investigation into the growth of the ovule of *Magnolia** from its earliest periods; he confines himself solely to the appearances seen in the different stages of its growth, which he illustrates by figures, without reference to any theory on the subject: those figures well accord with the explanation I have rendered of Mirbel's illustrations of the development of the ovule in *Aristolochia* and *Tulipa*; but there appears to me some little error in fig. 2, where the earliest pullulation is always somewhat excentric in instances of anatropy—never at the extreme tip, which would generate an atropal ovule.

I need not here recite the details of my own observations made in the spring of last year, upon the mode of growth of the anatropal ovule of *Amygdalus*†; suffice it to say that I have repeated them this year with the utmost care, from the very earliest periods of growth, and all that I had previously remarked is fully confirmed. I have noticed here, in every instance examined, as shown in the marginal figures, a deep depression completely upon one side (never at the extremity) of the wart-like pullulation from the placenta, which I have called the placentary sheath, because it encloses in its parenchyma the tracheal vessels of the future raphe, in the bottom of which hollow there is a small budding-point where the vessels terminate; and out of this point the nucleus originates, standing in the bottom of the hollow: this nucleus soon becomes surrounded by the annular rudiment of the secundine, while the margin of the depression by degrees expands into a cup of a horse-shoe form, the two arms of which abut upon and embrace a lamellar plate of the placenta, and the opposite extremity is rounded into a concentric form, surrounding and including the nucleus and secundine. In *Prunus* the wart-like protuberance is more globular than in *Amygdalus*; and upon one side, not far from the placenta to which it is attached, there is a very deep circular depression, in the bottom of which the diminutive nucleus is seen rising from the budding-point: this is gradually encircled by the secundine; and the deeply hollow support becomes first a cup, which finally grows down-

Figs. 1–7.

* "A short exposition of the structure of the ovule and seed of *Magnolia*," Journ. Linn. Soc. ii. 106.

† Ann. Nat. Hist. 3 ser. i. 359.

ward to form the primine, while its margin remains as the micropyle. Neither Mirbel's view nor Fritsche's notion is confirmed by my observations; the many cases I have seen convince me that the early growth of the nucleus and secundine proceeds wholly from the budding-point or future chalaza, which is the point of termination of the tracheal vessels imbedded in the substance of the main support or placentary sheath. This mode of growth is most conformable to the ordinary law of development, and is quite analogous to the production of the sepals, petals, stamens, disk, and ovary from the budding-point of the pedicel, which is furnished in like manner, and for the same purpose, with tracheal vessels. It is a far more reasonable inference than the gratuitous assumption of Fritsche, that the ovular tunics are generated by the spontaneous separation of the epidermis, which doubles itself up, so as to produce those tunics by its further expansion.

After this early period, the further increment is very evident: the bottom of the channel I have described, with the budding-point, grows *downward*, becoming by degrees an oblong pouch with a broad, open mouth, suspended by the funicular point of its origin, at the same time that the nucleus and secundine enclosed in it grow *upward*; this continues till we have a complete and suspended anatropal ovule, ready for impregnation, at which period the papillary apex of the nucleus is exposed within the open mouths of the tunics; during this successive growth of the ovule of *Amygdalus*, the apex of the nucleus never changes its zenithal aspect, while the chalaza as constantly points to the base of the cell; there is no one-sided growth of the tunics, which grow equally upon all sides; and there is no inversion of the nucleus or of its coats, according to the opinion generally entertained. In this development, all is beautifully contrived to attain by the most simple means the main function —the generation and perfection of the future embryo, for which purpose the apex of the nucleus is retained always in near proximity to the placenta by means of its short funicle; and close to this point we see, as Brongniart long since demonstrated, a lamellar plate, to which the funicle is attached, which plate, formed of a peculiar tissue, is terminated by a fringed border that overhangs the mouths of the ovular tunics: the articulated cells forming this process bear the name of *telæ conductrices*, because they serve to conduct the pollinic influence to the point of the nucleus, by which means the embryo-sac is impregnated. I mention here this point of structure, because the position of this fascicle of cells, in relation to the raphe, is sometimes an indication of importance, as I shall have to show in the case of the *Rhamnaceæ*.

The mode of origin and the changes that take place in the growth of campylotropal and amphitropal ovules, with some modifications, are quite analogous to all that occur in the anatropal; it is, therefore, unnecessary for our present purpose to speak of them; but in regard to atropal ovules, it is requisite to say a few words. Here the budding-point is at the very apex, not on one side of the placentary sheath; the nucleus therefore makes its first appearance in a depression at that point, where also the secundine soon surrounds it, while the extremity of the sheath is extended by degrees to form the primine,—all three growing straightforward in the same centrifugal direction; the chalazal point is consequently identical with the hilar or funicular point of attachment of the ovule, and therefore there exists in no case any simple raphe, and but rarely any tracheal vessels, except those which exist in the funiculus: the growth of the ovular tunics is just the same as in the anatropal ovules. Spiral vessels, however, are occasionally seen, extending radially beyond the region of the chalaza, through the tissues of the primine, as sometimes occurs in like manner in anatropal ovules.

In the foregoing details of an anatropal ovule, I have mentioned the raphe only as appearing in the shape of a simple cord imbedded in the tissues of the primine, traversing it upon its ventral side from the funicle to the chalaza, where it disappears. But other distinct kinds of raphe occur: it frequently happens that, besides the main cord just mentioned, other branches of the nourishing vessels, as they issue from the funicle, spread themselves in distinct nervures over the whole area of the testa: sometimes, as I have shown in the *Styraceæ*, these ramifications are extremely numerous, the delicate spiral threads being loose or in lax bundles, spread throughout the testa, like a fine web; this also occurs in the testa of *Ophiocaryon*, *Olea*, and many other seeds. In other cases, again, we find these ramifications radiating in distinct nervures from the chalaza and anastomosing over the surface of the seed; this is instanced in the Almond, to which Prof. Lindley has alluded as presenting an anomaly not readily accounted for; its nature is, however, easily explained. The Almond is generally described as being exalbuminous; for if we cut through the seed, we come immediately upon the large fleshy embryo, which is found enveloped by an apparently single flexible coating, but which on examination is seen to be composed of different integuments agglutinated together. The inner coating is easily detached by a blunt point introduced beneath it, by which means it may be separated entire; it is then very thin, almost membranaceous, opake, white, not reticulated, but apparently formed of minute aggregated cells, and perfectly homogeneous in all its parts; it is somewhat thickened over the

radicle, and comes away from the chalaza without discoloration, as easily as from all other parts of the surface; in fact, notwithstanding its attenuation, it presents all the characters of albumen. Intermediate between this and the external integument is a delicate membrane, which is separable with some difficulty, this being the tegmen, finely reticulated: the external testa is much thicker, opake, with a rugose surface. Upon raising the tegmen, we find, lying beneath it, several bundles of spiral threads in anastomosing bands, so loose that each fibre can be easily drawn out separately; these bundles of vessels constitute the branching raphe just described, the ramifications of which appear to issue from the chalaza, where the integuments are united in a solid disk. The source whence these vessels derive their origin in the chalaza may, however, be traced to the main cord of the raphe, which forms a thick bundle running from the hilum to the basal disk. The two integuments are so closely agglutinated together, that it is not easy to determine through which of them the branching portions penetrate; the main cord is manifestly in the outer tunic.

On two former occasions, I recorded two very unusual cases in which the raphe becomes entirely peripherical, that is to say, first runs in the usual manner up one side from the hilum to the chalaza, and then returns again along the opposite side of the seed to the hilum—in both directions in the form of a simple continuous cord: the one instance was in *Stemonurus**, a genus of the *Icacinaceæ*; the other appeared in *Cucurbitaceæ*†. I have yet to show that a similar abnormal course of the raphe is universal, as far as I have been able to ascertain, in *Rhamnaceæ*. The consideration of this peculiar development will be deferred till I have detailed all the curious circumstances connected with it, in a memoir just completed.

In the *Euphorbiaceæ*, the raphe, as a thick simple cord, runs in a straight line from the hilum to the opposite chalazal extremity, where it is imbedded in the outer tunic, which is sometimes as thick and fleshy as in *Magnolia*, and where, as in that genus, a distinct bony shell intervenes between that coating and the thin inner integument: this raphe perforates the shell through a small diapylar foramen, to reach a small chalaza at the base of that integument; and out of this chalaza I have sometimes observed other vessels distributed over the area of the tegmen, in ten or fewer radiating and almost parallel bands which extend from the base to the apex. The existence of an external arilline, in which the main cord of the raphe is im-

* Ann. Nat. Hist. 2 ser. x. 33; Contributions to Botany, i. p. 83, pl. 13; Trans. Linn. Soc. xxii. p. 98, pl. 19. figs. 6, 7, 8, 9.

† Trans. Linn. Soc. xxii. p. 92, pl. 19. figs. 47, 48, 49.

bedded, and which is often of a scarlet colour, is common to all the *Euphorbiaceæ*; and this is always more or less fleshy, and invariably invests the bony shell usually denominated the testa, but which shell, in all cases, I have found devoid of tracheal vessels.

The development of the ovule in its early stages is subject to many modifications, which, in different families of plants, are often constant; and these afford good characters, hitherto little noticed. Some interesting facts on this head were recorded by Mr. B. Clarke, eight years ago*, when he pointed out the importance of knowing the position of the raphe in its earliest development,—a character he employed to show the relation of different families in a systematic point of view, according to his own peculiar notions.

Prof. Agardh has very lately contributed a valuable collection of facts upon the same head, and with the same view, to which he has attached more importance than they deserve; still, the facts demonstrated by him claim our especial notice, as they are accompanied by nearly 500 figures illustrative of the modes of development of the ovule in 310 different genera of plants. He has shown how much the position of the raphe, in regard to the axis of the ovary, varies in different families, and even in different genera, of the same order; and in his novel systematic arrangement of Phanerogamia†, this difference has in many cases led him to break up many natural orders into distinct groups, which he separates by long intervals, while at the same time he places in juxtaposition other families of little real kindredship, thus suggesting a distribution quite incompatible with our generally received notions of real affinity. But although this new system is not likely to receive the support of botanists in general, still the many observations, and the numerous facts and drawings here contributed, will show the value of the character of the development of the ovule, if applied only as an accessory feature. In order, however, to elicit the true value of this character, it should be followed through all the changes of subsequent growth, up to the period of the perfection of the seed,—a consideration not attended to in that work. I have shown the importance of this last consideration in the *Styraceæ*, especially in the tribe *Halesieæ*; and I have yet to detail developments of a similar nature in other families which I have investigated. It

* "On the Position of the Carpels when 2, and when single; including Outlines of a new Method of Arrangement of the Orders of Exogens, and Observations on the Structure of Ovaries consisting of a single carpel." Proceed. Linn. Soc. ii. 105.—"On the Position of the Raphe in Anatropal Ovules," *ibid.* p. 147.

† Theoria Systematica Plantarum: Lundæ, 1858.

is with the view of extending this inquiry that I have brought together these remarks.

It is evident from the foregoing exposition that the word *anatropal*, as applied to an ovule developed under a certain condition, is a very incorrect term, and one that might with propriety be abolished, because it serves to perpetuate a prevailing error; but it may still be retained if we limit its signification to a comparative instead of an active sense,—meaning, by the word *inverted*, a different position of the radicle in regard to the hilum in anatropal seeds—not as expressing any action of gradual inversion of the nucleus and its tunics, as has been assumed.

I will now proceed to show that the development of the raphe is always normally ventral, or next the placenta, and that when it assumes a dorsal position, this is due exclusively to a resupination of the entire ovule. I have already explained the difference in the incipient development of an anatropal and an atropal ovule—that in the former the pullulation of the nucleus is never from the extreme point, but always more or less removed from it, and in general completely on one side of the placentary sheath; this is either on the upper or the lower face, but sometimes lateral, and in these cases the growth of the ovule is either downwards or upwards, or laterally in regard to the axis of the ovary, producing thus either pendent, ascending, or laterally horizontal ovules. When the first appearance of the nucleus is on the superior side of the funicular sheath, we have a pendulous ovule, with the raphe necessarily on the ventral side of the primine (as shown in the marginal figures in p. 19), in all cases where the point of its attachment upon the axis of the carpel is at any sufficient distance above the base of the cell to allow of its downward growth; but if this point of origin be contiguous to the base, then the downward extension of the primine, pressing against the bottom of the cell, causes the ovule to incline upwards gradually into an erect position (turning thus upon its funicle, as Mr. Brown first sagaciously demonstrated in the case of *Euonymus*), so that the ovule becomes completely reversed, with the raphe upon its dorsal face. In the same way, when the pullulation of the nucleus is upon the lower side of the funicular sheath, we have necessarily an ascending ovule with a ventral raphe, produced by the upward expansion of the sheath, as in the marginal figures, showing the first and two later stages of this growth, which prevails in all cases where the ovule has sufficient room to expand itself; but where this production of the funi-

Figs. 8–10.

cular support is close to the summit of the cell, then the pressure of growth causes the ovule to be forced round gradually upon its funicle till it becomes pendent, with its raphe in a dorsal position. In both these instances of resupination of the ovule, there is no removal of the mouths of the tunics from their close contiguity to thetelæ conductrices,—a very important feature in the history of its development. These two conditions of growth of the placentary sheath may be expressed by the terms *epipyla* and *hypopyla*,—the former from *ἐπὶ super*, *πύλη porta*, where the first development is upwards; and the latter from *ὑπὸ* et *πύλη*, where it shows itself on the lower side of the sheath. In the first condition (where the micropyle points upwards), we have an *ovulum anatropum epipylum*, or a pendent ovule with a ventral raphe; but where the same ovule becomes inverted by pressure, we have an *ovulum epipylum resupinatum*, or an ascending ovule with a dorsal raphe. Under the second condition (where the micropyle points downwards), we have an *ovulum anatropum hypopylum*, or an ascending ovule with a ventral raphe; but when this becomes inverted by pressure, it is an *ovulum hypopylum resupinatum*, or a pendent ovule with a dorsal raphe. It often happens, where numerous ovules issue from a placenta of limited extent, that we have erect, horizontal, and pendent ovules all crowded together, some with a ventral, others with a dorsal raphe; but it will be found that all are equally epipylous or equally hypopylous, the one series showing their raphes in their normal position, the second intermediately placed, while the third, by their resupination, have a dorsal raphe. Under the third condition, where the ovules are in collateral pairs, and where the earliest appearance of the nucleus is upon the lateral face of the placentary sheath, the raphes face one another, whether the subsequent direction of the ovule, by the pressure of growth, be pendent, horizontal, or ascending: this kind of development may be called *allopylar* if in a single ovule, and *heteropylar* when in collateral pairs.

Another consideration worthy of attention in the development of the ovule, is the position of the embryo in regard to the seminal tunics,—that is to say, whether one of the faces of the cotyledons, or whether its margins be placed opposite the raphe: this point has seldom been regarded, except where the embryo is amphitropal or campylotropal, in which cases this position is known, from the radicle being said to be incumbent or accumbent in regard to the cotyledons. This relative position is often a constant feature in certain families, while in others it is subject to much variation, as in *Rhamnaceæ*; and the character is even sometimes variable in the same genus, as in *Rhamnus*. The position of the face of the cotyledon in regard to the axis of the

ovary is a feature very distinct from that of its relation to the raphe; and the two should not be confounded together: thus in *Rhamnus catharticus* the raphe is dorsal, both with respect to the axis of the ovary and to the embryo; in *R. chlorophorus* it is dorsal with regard to the embryo, but lateral as respects the axis of the ovary. In most instances throughout the *Rhamnaceæ* the embryo is incumbent with respect to the ovary, one of its cotyledons being posterior, the other anterior, in regard to the axis; but it is accumbent in regard to the raphe, which skirts the margins of the cotyledons. In *Berchemia* the cotyledons are incumbent, both with regard to the ovary and to the dorsal raphe.

In this investigation, I have noticed only the proper integuments of the ovule, leaving out of consideration that coating which, after impregnation, frequently grows over the primine and produces in the seed either an incomplete or an entire tunic, called an *arillus*. Schleiden and others are of opinion that the true aril must necessarily be pervious at its extremity, and he concludes (*l. c.* p. 431) that wherever an actually closed structure surrounds the seed, it is undoubtedly a layer of the seed-coats: but this is mere opinion unsupported by proof; for it is equally probable that the aril may become closed just as much as the proper tunics of the ovule. It has also been thought that it must necessarily be fleshy; but I have shown* that it is often perfectly entire, and frequently hard and testaceous (as in *Canellaceæ*, *Winteraceæ*, &c.), in which case the true testa, or development of the primine, is generally either fleshy or membranaceous, contrary to its usually hardened condition.

Where, on the other hand (as in *Magnolia*, *Clusia*, &c.), the inner tunic of the ovule becomes hardened by osseous deposits, the primine, as in the former case, remains fleshy, and assumes the appearance of a complete arillus, for which reason I proposed to call it an *arilline*† instead of testa, to which name the hardened tunic is more entitled. It has been contended by Dr. Asa Gray that the osseous tunic and the aril-like covering which contains the cord of the raphe are both developed from the primine, the former resulting from hardened deposits upon its inner layers of cells, while the outer cells remain soft and fleshy. I have argued that, if such a deposition took place in the manner stated, these two dissimilar textures must be enclosed by a single epiderm and one endoderm; but we find, on the contrary, each of the tunics provided with its respective external and internal epidermis, showing that the two formations are independent in their origin. It is also clear, that if these

* Ann. Nat. Hist. 3 ser. ii. 39; Contributions to Botany, i. 128.

† Trans. Linn. Soc. xxii. p. 89.

two coatings, so very dissimilar in their nature, were produced from a single ovular tunic, then the cord of the raphe ought rather to be found in the nut, as that would correspond with the inner layers of mesodermic tissue in which the raphe exists in the primine; whereas that cord of vessels is really imbedded in the fleshy tunic, while the nut is free from vessels of any kind. This is further shown in the general structure of the seed of *Magnolia*, where the raphe passes in its usual course through the tissues of the fleshy coating, from the base to the apex, when it suddenly breaks through the endoderm, and arrives at a distinct foramen in the chalazal extremity of the nut, which I have called a diapyle, through which it passes, and soon becomes lost in the thickened areole or chalaza of the inner integument.

On the other hand, we may conclude either that the nut originates in a development of the secundine, and that the tegmen results from the tercine or membrane of the nucleus (which is a very rational inference), or that the nut is of independent origin (which is still within the range of probability). Indeed there is nothing to prevent the possibility or probability of the formation of an intraneous coat between the usual tunics in the growing seed, subsequently to the closing of the micropyle of the ovule. We frequently meet with a copious deposit of loose cellular tissue between the testa and tegmen, or even between the latter and the albumen; and this deposition may become consolidated into a distinct membrane, or hardened by solid deposits: wherever there exists a budding-point, this may at any time take place. We have proof of the actual formation of such a tunic between the primine and secundine in the *Gnetaceæ**; and this, if applied to the case of *Magnolia*, points to a far more probable cause for the appearance of the hard tunic in the seed, than the improbable suggestion of Schleiden and Gray, to which I have just referred.

Schleiden, although entertaining so many ideal fancies respecting developments, gives nevertheless a somewhat true account of the present state of our knowledge on this subject: he says (*l. c.* p. 427)—"A greater confusion than that which prevails in the theory of the seed-coats is scarcely conceivable; the most heterogeneous things are thrown together under one name; thoroughly identical ones are placed in different kinds of organs; and there is nothing for it, if we would not make greater confusion, but to cut the thread and begin over again: the epidermis of the seed is sometimes described as testa, sometimes as arillus; seed-membranes are introduced where no true integuments exist."

* According to the interesting details given by Griffith, Lindley's 'Vegetable Kingdom,' p. 233, where analytical figures demonstrate the fact.

My object in bringing together the facts related in the foregoing pages is to show that we may always proceed with some degree of certainty, if we never lose sight of positive, invariable landmarks. Beyond doubt the surest course is to trace the developments from the earliest growth of the ovule to the final perfection of the seed; but where this cannot be done, notwithstanding the variable texture and condition of the tunics developed from the growth of the primine and secundine, we may always, with much confidence, by attending to the unerring indications afforded by the raphe, generally deduce the true nature and origin of the different coatings of seeds in Phanerogamous plants.

III.—*On* Dracunculus *and Microscopic* Filaridæ *in the Island of Bombay.* By H. J. Carter, Esq., Bombay.

[With three Plates.]

In the month of October 1853, I published a "Note" on *Dracunculus* in the island of Bombay*, and in February 1858 communicated additional "Observations" on the same subject†, in order to correct and complete it. My object in the first communication was to give an anatomical description of the Guinea-worm of this island; to compare it and its young one with that microscopic species of the Filaridæ which is most common in the fresh-water tanks here, to which I have applied the name of "Tank-worm;" to try to account for the origin of *Dracunculus*; and to suggest some prophylactic measures for its prevention. This led me to a further study of the microscopic species, both in the fresh and brackish or salt waters of the island, which again threw my attention back upon *Dracunculus*, and has finally ended in making me acquainted, not only with much more of the anatomy of the latter, but with nearly the whole of the organology, formation of the ova and spermatozoa of the Tank-worm, as well as with several other microscopic species, all of which are interesting in various ways, but of which I have not been able to obtain much more than the external forms.

In my last communication, viz. the "Observations," I gave a short summary of the latter researches; and I now propose to give the full paper, with illustrations.

It may be conceived, perhaps, that much has been written on the Guinea-worm, and that publishing anything more about it is superfluous; but what has been written is very little to the purpose, and it is for this reason that it is desirable to record a

* Transactions Med. and Phys. Soc. Bombay, No. 2. p. 45, new series.
† Annals, vol. i. p. 410, 1858.